



AGRICULTURAL AND FOREST METEOROLOGY

Agricultural and Forest Meteorology 122 (2004) 129-137

www.elsevier.com/locate/agrformet

# Yield responses of southern US rice cultivars to CO<sub>2</sub> and temperature

Jeffrey T. Baker\*

USDA-ARS Cropping Systems Research Laboratory, 302 West 1-20, Big Spring, TX 79720, USA Received 9 June 2003; received in revised form 29 September 2003; accepted 29 September 2003

### **Abstract**

Previous studies on the effects and interactions of atmospheric carbon dioxide concentration ([CO<sub>2</sub>]) and air temperatures have shown large differences in growth and yield responses among Asian rice (Oryza sativa L.) cultivars. Far less attention has been focused on rice cultivars commonly grown in the Southern US. This 2-year study was conducted to determine the effects of [CO<sub>2</sub>] and air temperature on four Southern US rice cultivars. In 2000, 'Cocodrie', 'Cypress', and 'Jefferson' were grown season-long in five outdoor, naturally sunlit, controlled-environment chambers in constant day-night air temperature regimes of 24, 28, 32, 36, and 40 °C under an elevated [CO<sub>2</sub>] of 700 µmol mol<sup>-1</sup>. In 2000, an additional chamber containing all three cultivars was maintained at 28 °C and an ambient [CO<sub>2</sub>] treatment of 350 µmol mol<sup>-1</sup>. In 2002, a more detailed study examining both main crop (MC) and ratoon crop (RC) yields was conducted with the rice cultivar 'Lamont' in these same chambers with day-night air temperature treatments of 19/15, 23/19, 27/23, 31/27, and 35/31 °C under an elevated [CO<sub>2</sub>] of 700 µmol mol<sup>-1</sup>. In 2002, an additional chamber was maintained at 27/23 °C and an ambient [CO<sub>2</sub>] treatment of 350 µmol mol<sup>-1</sup>. In the 2000 experiment, all the plants of all three cultivars in the 40 °C treatment died during early vegetative growth. In the constant 36 °C air temperature treatment, all three cultivars survived to produce panicles but failed to produce any seed yield. At the 28 °C temperature treatment, CO2 enrichment increased grain yield by 46-71% among the three cultivars with the cultivar Cypress being the most responsive to CO<sub>2</sub> enrichment. In the 2002 experiment with the cultivar Lamont, plants in the 35/31 and 19/15 °C treatments survived to produce panicles but failed to produce any seed yield. In the 27/23 °C treatment, CO2 enrichment resulted in a non-significant increase in seed yield for the MC but more than doubled RC yields. Comparisons of these results with findings from prior studies on Asian indica and japonica cultivars indicate that these Southern US rice cultivars may be more sensitive to high temperature stresses during reproductive development than previously studied Asian cultivars. These results also point to the possibility of selecting or breeding rice cultivars with enhanced capability to take advantage of future global increases in  $[CO_2]$ .

Published by Elsevier B.V.

Keywords: Atmospheric carbon dioxide; Oryza sativa; Climate change

# 1. Introduction

Atmospheric carbon dioxide concentration ([CO<sub>2</sub>]) was about 358 μmol mol<sup>-1</sup> in 1995 and is currently increasing by about 1.6 μmol mol<sup>-1</sup> per year or nearly 0.5% per year (Keeling et al., 1995). This increase in

<sup>\*</sup> Tel.: +1-915-263-0293; fax: +1-915-263-0293. E-mail address: jtbaker@lbk.ars.usda.gov (J.T. Baker).

[CO<sub>2</sub>] and other radiatively active gasses, has led to predictions of future increases in global air temperatures (IPCC, 2001). Work by Jones et al. (1994, 1999) and Mann et al. (1999) suggest that there has been a 0.3–0.6 °C warming of the earth's surface since the late 19th century.

Globally, rice is the single most important food crop in terms of direct human food consumption. A number of studies have been conducted to examine the effects of combinations of air temperature and [CO<sub>2</sub>] on Asian rice cultivars (Baker et al., 1992; Allen et al., 1995; Mathews et al., 1995; Ziska et al., 1996; Horie et al., 2000) while far less attention has been devoted to rice cultivars grown in the United States. Rice is a C<sub>3</sub> crop species and generally responds favorably to carbon dioxide enrichment with increased assimilation rates and final grain yield. However, several studies have shown that high air temperatures can reduce grain yield even under carbon dioxide enrichment (Baker and Allen, 1993; Ziska et al., 1997; Horie et al., 2000) due to problems with the pollination process leading to increased spikelet sterility (Yoshida, 1981; Matsui et al., 1997). At even higher temperatures, female sterility can also occur (Satake and Yoshida, 1978). Summarizing a series of experiments, Baker and Allen (1993) reported a temperature optimum of 26 °C for grain yield of the indica-type rice cultivar IR-30. In those experiments, grain yields declined by about 10% per each 1 °C increase in average day-night air temperature beyond 26°C and reached zero yield at 36 °C. In those experiments, temperature was expressed as an average of day-night air temperature treatments and adjusted for thermoperiod.

Recent studies indicate that the relative enhancement of rice yields due to CO<sub>2</sub> enrichment is progressively reduced with increases in air temperatures (Kim et al., 1996; Matsui et al., 1997). Although the exact mechanism by which CO<sub>2</sub> enrichment renders the rice flowering process more sensitive to high air temperatures is unknown at present, a reduction in transpirational cooling under CO<sub>2</sub> enrichment has been suggested as one possibility (Matsui et al., 1997; Horie et al., 2000). There appears to be considerable variability among current rice cultivars in their responses to [CO<sub>2</sub>] and temperature (Ziska and Teramura, 1992; Ziska et al., 1996; Moya et al., 1998) leading to the possibility of selecting rice cultivars against these two environmental variables for yield

increases and/or stability in a possibly warmer, but almost certainly higher future CO<sub>2</sub> world.

Rice ratooning is practiced in many of the rice growing regions of the Southeastern US. This practice involves harvesting the main crop (MC) and allowing the crop to re-grow for a second or ratoon crop (RC). Although RC yields are typically about one-third lower than that of the MC, production costs are considerably reduced compared to the MC (Bollich and Turner, 1988). To my knowledge, no previous work has examined the effects of CO<sub>2</sub> enrichment on RC yields. My goals were to evaluate the grain yield and yield component responses of four rice cultivars commonly grown in the Southern US to a range of air temperature treatments under CO<sub>2</sub> enrichment.

## 2. Materials and methods

# 2.1. Controlled-environment chambers

This experiment was conducted in the recently constructed Soil-Plant-Atmosphere-Research (SPAR) facility at Beltsville, MD. This facility is comparable in design and operation to similar experimental systems at the University of Florida (Pickering et al., 1994), Corvallis, OR (Tingey et al., 1996) and Mississippi State University (Reddy et al., 2001). This facility consists of 18 naturally sun-lit, SPAR chambers, six of which were available for use in these experiments. These SPAR chambers consist of clear acrylic chambers and are 2.3 m tall, 1.5 m<sup>2</sup> in cross-sectional area with a total chamber volume of 33601. Excluding the internal ducting, the space available for growing plants is 1.0 m<sup>2</sup>. Air was constantly re-circulated within the chamber in a closed loop at about  $3 \,\mathrm{m \, s^{-1}}$ . The facility includes a dedicated Sun SPARC 5 work station (Sun Microsystems, Inc., Mountainview, CA)<sup>1</sup> used to control [CO<sub>2</sub>] in each chamber and record plant responses (photosynthesis, evapotranspiration) and environmental data (air and soil temperatures, humidity, [CO<sub>2</sub>], and solar radiation) every 300 s. Air temperature and relative humidity are monitored and controlled with TC2 controllers (Environmental Growth Chambers, Inc., Chagrin Falls, OH). Air temperatures

<sup>&</sup>lt;sup>1</sup> Mention of this or other proprietary products is for the convenience of the readers only, and does not constitute endorsement or preferential treatment of these products by USDA-ARS.

were measured with shielded, aspirated thermocouples while paddy water temperatures were measured with submerged thermocouples, at 30 s intervals and averaged and recorded every 300 s. Constant humidity was maintained by operating solenoid valves that injected chilled water through the cooling coils located in the air handler of each chamber. These cooling coils condensed excess water vapor from the chamber air in order to regulate relative humidity at 60%.

Gas sample lines for measuring chamber and ambient air [CO<sub>2</sub>] were run underground from each chamber to the field laboratory building. Each chamber [CO<sub>2</sub>] was measured with a dedicated infrared gas analyzer (LI-COR Model LI- 6252, Lincoln, NE). Moisture was removed from the gas sample by running the sample lines through a refrigerated water trap (4°C) that was automatically drained once each hour. Chamber [CO2] was maintained by supplying pure CO2 from a compressed gas cylinder to mass flow controllers (Omega Engineering, Inc, Stanford, CT) located in the air ducting in each chamber using a feed-forward, feed-back proportional-integral-differential (PID) control algorithm similar to the one described by Pickering et al. (1994). Grey polypropylene screen shades were maintained from the chamber floor to the top of the plant canopy in order to provide a light environment similar to that found in a field crop.

# 2.2. Plant culture 2000

The soil used in both experiments was an enhanced rice soil that was mixed on 15 July 1986 as follows: 21 cubic yards of dark red Christiana clay top soil was mixed with 8.4 m<sup>3</sup> of composted cow manure, 39 kg of 5-10-5 fertilizer and 108 kg of high magnesium dolomite lime. Pre-plant soil tests indicated high levels of N-P-K, adequate levels of soil micro-nutrients and a pH of 6.7. This soil was steam sterilized prior to placement into plastic containers 18.91 in volume and 0.4 m tall. Prior to planting rice, each container was filled with soil to within 0.07 m of the container top in order to allow the later application of a 0.05 m permanent flood above the soil surface. Water was supplied to each container with a computer-controlled drip irrigation system. Additional N as urea was applied at a rate of 4 g per container on 16 August 2000. The Southern US rice cultivars utilized in 2000 were

'Cocodrie', 'Cypress', and 'Jefferson'. These cultivars are commonly grown in the rice growing regions of Texas and Louisiana, USA. Three plastic containers per cultivar (nine containers total per chamber) were placed into the chambers on the day of planting. The nine containers per chamber were arranged in three rows of three containers, simulating a  $0.3 \times 0.3$  hill arrangement with a combined total of 36 plants m<sup>-2</sup> after thinning. Eight seeds per container for each cultivar were planted on 29 June 2000. The rice was thinned to four plants per container on 10 July and the 0.05 m flood water was applied. All six chambers were maintained at a constant day–night air temperature of 30 °C until 7 July to facilitate uniform emergence.

Five chambers were maintained from planting to final harvest at a daytime [CO2] treatment of 700 μmol CO<sub>2</sub> mol<sup>-1</sup> air while one additional chamber was controlled to 350 µmol CO<sub>2</sub> mol<sup>-1</sup>. Constant day-night air temperature treatments of 24, 23, 32, 36, and 40 °C were initiated in the 700 µmol mol<sup>-1</sup> [CO<sub>2</sub>] treatment on 7 July while the 350  $\mu$ mol mol<sup>-1</sup> [CO<sub>2</sub>] treatment was controlled to 28 °C. Average measured air temperatures (mean  $\pm$  S.D.) were  $24.7 \pm 0.14$ ,  $28.0 \pm 0.05$ ,  $31.5 \pm 0.14$ , and  $36.5 \pm 0.05$ for the 24–36 °C temperature treatments, respectively. Plants in the 40 °C temperature treatment died during early vegetative growth and the air temperature and [CO<sub>2</sub>] treatments were terminated in this chamber. Average [CO<sub>2</sub>] for the remaining chambers was  $358 \pm 4.1$  and  $705 \pm 6.3 \,\mu \text{mol mol}^{-1}$  for the 350 and 700 µmol mol<sup>-1</sup> [CO<sub>2</sub>] treatments, respectively.

The plants were harvested at 26 and 28 September and 10 and 19 October for the 28, 32, 36, and 24 °C temperature treatments, respectively, in the 700 µmol mol<sup>-1</sup> treatment. The 350 µmol mol<sup>-1</sup> 28 °C treatment was harvested on 27 September. At maturity, each plant was detached at ground level and the numbers of living leaves, tillers, and panicles were counted. Dry weights were determined separately for each plant part after oven drying at 70 °C for at least 48 h. Panicle weight, grain weight, and grain number were determined after oven drying and threshing the panicles on each plant.

## 2.3. Plant culture 2002

Seeds of the rice cultivar "Lamont" were sown in greenhouse flats (cell size  $6.0 \text{ cm} \times 6.0 \text{ cm} \times 6.0 \text{ cm}$ )

filled with a commercial peat–vermiculite mix on 17 April 2002. Twelve seedlings with about 1.5 main-stem leaves were transplanted into each of nine containers within each of the six outdoor controlled-environment chambers on 26 April. Plants were thinned to a uniform eight plants per container by removing two plants from each container on both 6 and 20 May. This resulted in a final plant population of 72 plants m<sup>-2</sup> in each chamber.

A constant day–night air temperature of 30 °C was maintained from 26 to 29 April to promote uniform establishment. The [CO<sub>2</sub>] treatments were initiated on 26 April and air temperature treatments were imposed on 29 April air. Five chambers were maintained from 29 April to final harvest at a daytime [CO<sub>2</sub>] treatment of 700  $\mu$ mol CO<sub>2</sub> mol<sup>-1</sup> air while one additional chamber was controlled to 350  $\mu$ mol mol<sup>-1</sup> and 27/23 °C. In the 700  $\mu$ mol mol<sup>-1</sup> [CO<sub>2</sub>] treatment, day–night air temperature treatments were set to 19/15, 23/19, 27/23, 31/27, and 35/31 °C. The day–night thermoperiod for this experiment was 15/9 h.

Due to slow growth and development, the  $19/15\,^{\circ}\mathrm{C}$  treatment failed to re-grow a RC. The MC of the  $19/15\,^{\circ}\mathrm{C}$  was harvested on 23 October. The MC/RC harvest dates were: 13 August/31 October at  $23/19\,^{\circ}\mathrm{C}$ ; 30 July/11 October at  $27/23\,^{\circ}\mathrm{C}$ ; 30 July/4 October at  $31/27\,^{\circ}\mathrm{C}$ ; 19 August/23 October at  $35/31\,^{\circ}\mathrm{C}$  for the  $700\,\mu\mathrm{mol\,mol^{-1}}$  [CO<sub>2</sub>] treatment. For the  $350\,\mu\mathrm{mol\,mol^{-1}}$  [CO<sub>2</sub>] treatment maintained at

27/23 °C, MC/RC harvest dates were 2 August/16 October MC and RC yield and yield components were measured as described previously for the 2000 experiment with one exception. To allow re-growth of the RC crop, at MC harvest the plants were cut at 0.2 m above the soil surface. Due to the very short plant height in the 19/15 °C treatment, these plants were cut at 0.1 m above the soil surface. Above ground biomass and harvest index were based on biomass above these cuffing heights for both the MC and RC.

In both experiments, growth and yield measurements were made for each individual container. Each container was considered a replicate in a completely random experimental design. The data were analyzed by analysis of variance using the GLM procedure provided by the SAS Institute (Cary, NC).

#### 3. Results

# 3.1. Yield 2000

Shown in Table 1 are the yield and yield components for the 350 and  $700 \,\mu\mathrm{mol} \,\mathrm{mol}^{-1}$  treatments grown at  $28\,^{\circ}\mathrm{C}$  in the 2000 experiment. The effects of  $\mathrm{CO}_2$  enrichment on grain yield amounted to gains of 46, 71, and 57% for Cocodrie, Cypress, and Jefferson, respectively. The  $\mathrm{CO}_2$  enrichment increased grain yield largely through increases in the number of

Table 1 Grain yield, components of yield, and growth measurements made at final harvest for three US rice cultivars grown at  $28\,^{\circ}$ C and two  $CO_2$  concentrations

$CO_2$ $(\mu \text{mol mol}^{-1})$	Cultivar	Grain yield (g per plant)	Panicles per plant (no. per plant)	Filled grain per panicle (no. per panicle)	Grain mass (mg per seed)	Above ground biomass (g per plant)	Harvest index
350	Cocodrie	14.5	11.2	71.2	18.3	50.1	0.29
	Cypress	18.0	15.4	63.3	18.5	61.9	0.29
	Jefferson	12.8	9.6	67.3	19.3	44.1	0.29
700	Cocodrie	21.2	13.8	82.8	19.1	70.1	0.31
	Cypress	30.8	16.8	89.3	20.7	90.5	0.34
	Jefferson	20.1	10.2	92.9	21.2	59.4	0.34
F-values							
	$CO_2$	14.9**	2.8 NS	22.2**	7.0*	10.9**	9.1*
	Cult	4.5*	15.5**	0.3 NS	2.2 NS	5.0*	1.1 NS
	$CO_2\timesCult$	0.7 NS	0.4 NS	1.1 NS	0.5 NS	0.4 NS	0.7 NS

NS, not significant.

<sup>\*</sup> Significant at the 0.05 probability levels.

<sup>\*\*</sup> Significant at the 0.01 probability levels.

Table 2 Grain yield, components of yield, and growth measurements made at final harvest for three US rice cultivars grown at elevated  $CO_2$  and five air temperature treatments

Cultivar	Temperature (°C)	Grain yield (g per plant)	Panicles per plant (no. per plant)	Filled grain per panicle (no. per panicle)	Grain mass (mg per seed)	Above ground biomass (g per plant)	Harvest index
Cocodrie	24	20.1	13.7	74.5	19.9	67.6	0.28
	28	21.2	13.8	82.8	19.1	70.1	0.31
	32	19.5	12.7	68.7	22.2	66.8	0.28
	36	0.0	13.3	0.0	_	34.2	0.00
	40	0.0	0.0	_	_	0.0	_
Cypress	24	14.8	20.6	34.0	21.6	76.1	0.20
	28	30.8	16.8	89.3	20.7	90.5	0.34
	32	21.3	14.3	66.4	22.4	81.4	0.26
	36	0.0	9.6	0.0	_	29.1	0.00
	40	0.0	0.0	_	_	0.0	-
Jefferson	24	20.1	14.3	55.7	24.2	71.8	0.27
	28	20.1	10.2	92.9	21.2	59.4	0.34
	32	16.6	10.4	61.5	24.9	57.7	0.28
	36	0.0	11.1	0.0	_	28.2	0.00
	40	0.0	0.0	_	_	0.0	-
F-values							
	Cult	0.7 NS	2.5 NS	2.0 NS	25.3**	2.9 NS	1.4 NS
	Temp	51.4**	25.4**	140.7**	21.8**	67.8**	181.7**
	Cult × Temp	1.3 NS	1.1 NS	3.5*	2.0 NS	1.3 NS	1.5 NS

NS, not significant.

filled grains per panicle and an increase in individual seed mass of about 1–2 mg per seed. The CO<sub>2</sub> enrichment also increased above ground biomass and harvest index. Among three cultivars, Cypress had the highest grain yield due mainly to the production of more panicles per plant compared with the other two cultivars.

As expected, the temperature treatments had large effects on growth and yield (Table 2). In all three cultivars, the plants in the 40 °C treatment died during vegetative growth and there was no living above ground biomass at final harvest. Plants in the 36 °C treatment survived to produce panicles, but none of the panicles in this treatment produced grain for any of the three cultivars. The 28 °C temperature treatment appeared to be closest to the optimum temperature for grain yield, filled grain numbers, above ground biomass, and harvest index. As with the [CO<sub>2</sub>] treatments (Table 1), filled grains per panicle was the most important yield component contributing to grain yield among the air temperature treatments (Table 2).

## 3.2. Yield 2002

For the cultivar Lamont in the  $27/23\,^{\circ}\text{C}$  treatment,  $\text{CO}_2$  enrichment resulted in a non-significant 12% increase in MC seed yield (Table 3). All other MC growth and yield measurements were similarly unaffected by  $\text{CO}_2$  enrichment except for filled grain number per panicle which was barely significantly higher ( $P \leq 0.05$ ) than filled grain number of the ambient [ $\text{CO}_2$ ] treatment. Temperature effects on MC yield and yield components were large. Plants in both the 19/15 and 35/31  $^{\circ}\text{C}$  temperature treatments survived to produce panicles but failed to fill any grain. Both MC grain yield and numbers of filled grains per panicle were highest in the  $27/23\,^{\circ}\text{C}$  temperature treatments.

In contrast to the MC yields, RC yields were roughly doubled by CO<sub>2</sub> enrichment at the 27/23 °C temperature treatment (Table 4). Significant increases in number of filled grains per panicle and individual seed mass were the most important components contributing to the doubling of RC yields by CO<sub>2</sub> enrichment.

<sup>\*</sup> Significant at the 0.05 probability levels.

<sup>\*\*</sup> Significant at the 0.01 probability levels.

Table 3
Main crop grain yield and components of yield for the rice cultivar 'Lamont' grown in five day–night air temperature treatments and two atmospheric CO<sub>2</sub> concentrations

$CO_2$ $(\mu \text{mol mol}^{-1})$	Temperature (°C)	Grain yield (g per plant)	Panicles per plant (no. per plant)	Filled grain per panicle (no. per panicle)	Grain mass (mg per seed)	Above ground biomass (g per plant)	Harvest index
350	27/23	16.9	9.7	81.9	20.6	33.7	0.53
700	19/15	0.0	12.1	0.0	0.0	22.4	_
	23/19	8.9	12.6	34.3	19.7	28.1	0.29
	27/23	19.0	8.7	101.4	21.6	33.5	0.57
	31/27	14.4	9.9	62.3	23.0	34.5	0.41
	35/31	0.0	8.9	0.0	0.0	22.4	_
	LSD (Temp)*	3.4	1.4	12.7	1.0	5.0	0.07
	LSD (CO <sub>2</sub> )**	NS	NS	18.3	NS	NS	NS

<sup>\*</sup> Least significance difference (LSD) with *P*-value  $\leq$ 0.05 for comparing means among the five air temperature treatments (LSD (Temp)) at a CO<sub>2</sub> concentration of 700  $\mu$ mol mol<sup>-1</sup>.

Table 4
Ratoon crop grain yield and components of yield for rice cultivar 'Lamont' grown in four day-night air temperature treatments and two atmospheric CO<sub>2</sub> concentrations

$CO_2$ ( $\mu$ mol mol $^{-1}$ )	Temperature (°C)	Grain yield (g per plant)	Panicles per plant (no. per plant)	Filled grain per panicle (no. per panicle)	Grain mass (mg per seed)	Above ground biomass (g per plant)	Harvest index
350	27/23	5.6	8.8	36.8	17.3	18.9	0.29
700	23/19	4.6	17.2	12.9	21.5	19.7	0.24
	27/23	11.4	9.6	58.2	20.8	24.7	0.46
	31/27	13.4	16.7	37.5	21.6	31.9	0.42
	35/31	0.0	17.5	0.0	0.0	22.8	_
	LSD (Temp)*	1.6	3.2	4.5	0.7	3.8	0.03
	LSD (CO <sub>2</sub> )**	2.0	NS	7.7	1.8	3.5	0.05

<sup>\*</sup> Least significance difference (LSD) with P-value  $\leq$ 0.05 for comparing means among the four air temperature treatments (LSD (Temp)) at a CO<sub>2</sub> concentration of 700  $\mu$ mol mol<sup>-1</sup>.

Above ground biomass and harvest index were also significantly increased by CO<sub>2</sub> enrichment. In both the MC (Table 3) and RC (Table 4) plants in the 35/31 °C temperature treatment survived to produce panicles but failed to fill any seed. The RC yields and above ground biomass were significantly larger in the 31/27 °C treatment compared with the other temperature treatments.

# 4. Discussion

To date, the majority of CO<sub>2</sub> enrichment studies on rice have been conducted on Asian rice cultivars. In many of these studies, CO<sub>2</sub> enrichment increased grain yield largely through an increase in tillering and panicle numbers (Imai et al., 1985; Baker and Allen, 1993; Kim et al., 1996; Ziska et al., 1996; Kim et al., 2001). For example, Moya et al. (1998) found that grain yield enhancements due to CO<sub>2</sub> enrichment among three different Asian cultivars was related to relative tillering ability of a particular cultivar. In their study, the 'new plant type' (NPT2) cultivar, had a relatively fixed tiller number with large panicles, and was the least responsive cultivar to CO<sub>2</sub> enrichment. However, Sheehy et al. (2001) argues that a high tillering ability is not a desirable trait in a high yield environment because this trait increases susceptibility to lodging.

<sup>\*\*</sup> Least significance difference (LSD) with P-value  $\leq 0.05$  for comparing means between the two atmospheric CO<sub>2</sub> treatments at an air temperature treatment of 27/23 °C.

<sup>\*\*</sup> Least significance difference (LSD) with P-value  $\leq 0.05$  for comparing means between the two atmospheric CO<sub>2</sub> treatments at an air temperature treatment of 27/23 °C.

In the present study with Southern US rice cultivars, CO<sub>2</sub> enrichment did not significantly affect final numbers of panicles (Tables 1, 3 and 4). Here, the number of filled grains per panicle was the largest yield component contributor to increased grain yield under CO<sub>2</sub> enrichment followed in most cases by a modest but significant increase in individual seed mass.

These differences in yield component compensation between Asian and Southern US rice cultivars in response to CO<sub>2</sub> enrichment could be influenced by differences in plant population, not only between Asian and Southern US rice production systems but also by the plant populations used in this study. In Asia, rice is often transplanted by hand into hills and plant populations of 50–75 plants m<sup>-2</sup> are common. In the US, rice is usually drill seeded into rows and plant populations of 100-150 plants m<sup>-2</sup> are typical. The plant populations of 36 and 72 plants m<sup>-2</sup> used in this study are more typical of Asian transplanted rice rather than direct seeded rice in the US. Plant population plays an important role in yield component formation because, as with most small grain cereals including rice, tillering and final numbers of panicles per plant typically decrease with increasing plant population and competition for light. However, even at the lower plant populations used in this study, CO2 enrichment did not significantly increase panicle numbers while yield increases due to CO2 enrichment were realized mainly by increases in number of seeds per panicle. This result may reflect a genetic control of tillering for these US rice cultivars and/or the use of shade screens maintained at canopy height around the outside of the chambers designed to simulate the light environment found in a field crop.

The large RC yield increase from CO<sub>2</sub> enrichment (Table 4) was anticipated prior to the experiment. In rice, remobilization of stored carbohydrates in the leaves and stem can contribute between 20 and 40% of the MC grain yield (Yoshida, 1972; Murata and Matsushima, 1975). Turner and Jund (1993) found a positive correlation between MC stem total non-structural carbohydrate (TNC) content measured at MC harvest and subsequent RC grain yields. They suggested that high MC stem TNC should contribute to RC yields through beneficial effects on tiller regeneration processes following MC harvest. Several studies have shown that CO<sub>2</sub> enrichment increases rice sucrose, starch, and TNC concentra-

tions in vegetative tissues (Rowland-Bamford et al., 1990; Vu et al., 1998; Widodo et al., 2003). In addition to elevated TNC content, CO<sub>2</sub> enrichment also stimulates canopy photosynthesis. Thus, CO<sub>2</sub> enrichment would be expected to result in increased RC yield from a combination of increased TNC content of both the MC and RC as well as higher canopy photosynthetic rates during the RC grain filling period.

The failure of Lamont to produce any seed yield in the 19/15 °C is not surprising since it is well established that cool temperatures below 20 °C can result in spikelet sterility due to failure of pollen development at the microspore stage (Sasake and Hayase, 1970) or by injury sustained at flowering (Abe, 1969). Yield reductions caused by high temperature stresses are more relevant to the study of the effects of elevated [CO<sub>2</sub>] and potential future climate change. As daily mean temperatures increased above 26 °C, rice grain yields were progressively reduced in both an *Indica* cultivar ('IR-30', Baker and Allen, 1993) and a *Japonica* cultivar ('Akihikari', Kim et al., 1996). As flowering in rice usually occurs near midday, daytime maximum air temperature, rather than average daily temperature, is more relevant to the consideration of high temperature induced spikelet sterility. In these two previous studies, daytime air temperatures at or above 40-41 °C resulted in zero grain yield. However, some yield was still produced at daytime air temperatures of 37 °C (Baker and Allen, 1993) or as high as 39–40 °C (Kim et al., 1996). The results presented here (Tables 1–4) indicate that the upper daytime air temperature threshold for grain yield of these four US rice cultivars is somewhere between 32 and 35 °C. It should be emphasized that this upper temperature threshold range was obtained for [CO<sub>2</sub>] enriched plants. Recent work indicates that CO2 enrichment increases spikelet susceptibility to high temperature induced sterility (Kim et al., 1996; Matsui et al., 1997). The exact mechanism for this effect is unknown but reduced transpirational cooling under CO<sub>2</sub> enrichment has been suggested as one possibility (Horie et al., 2000). Other environmental factors including wind speed and humidity as well as temperatures a few days prior to flowering (Matsui et al., 1997) have also been shown to affect the magnitude of high temperature induced spikelet sterility. Ziska et al. (1996) have shown that increasing nighttime air temperature treatments can also reduce seed set and grain yields even when daytime air temperatures were held constant.

## 5. Conclusions

The wide range in grain yield responsiveness to CO<sub>2</sub> enrichment found among these four US rice cultivars points to the potential for selecting or developing high yielding US rice cultivars with the ability to take advantage of expected future global increases in [CO<sub>2</sub>]. The findings presented here indicate that CO<sub>2</sub> enrichment could have potentially large positive effects on RC yields. Comparison of the results presented here with prior studies suggests that under CO<sub>2</sub> enrichment, these four US rice cultivars may be more sensitive to high temperature stresses than previously studied Asian *indica* and *japonica* cultivars.

# Acknowledgements

I thank Robert Jones, Jackson Fischer, and Geetha Reddy for their valuable assistance.

# References

- Abe, I., 1969. Agro-meterological studies reguarding the effect of easterly winds ('Yamase wind') on the growth of rice plants in Aomori prefecture. Bull. Aomori Agricult. Exp. Station 14, 40–138 (In Japanese).
- Allen Jr., L.H., Baker, J.T., Albrecht, S.L., Boote K.J., Pan, D., Vu, J.C.V., 1995. Carbon dioxide and temperature effects on rice. In: Peng, S., Ingram, K.T., Neue, H.-U., Ziska, L.H. (Eds.), Climate Change and Rice. Springer–Verlag, Berlin, pp. 258–277.
- Baker, J.T., Allen Jr., L.H., Boote, K.J., 1992. Temperature effects on rice at elevated CO<sub>2</sub> concentration. J. Exp. Bot. 43, 959–964.
- Baker, J.T., Allen Jr., L.H., 1993. Contrasting crop species responses to CO<sub>2</sub> and temperature: rice, soybean, and citrus. In: Rozema, J., Lambers, H., Van de Geijn, S.C. (Eds.), CO<sub>2</sub> and Biosphere. Elsevier, Amsterdam, pp. 239–260.
- Bollich, C.N., Turner, F.T., 1988. Commercial ratoon rice production in Texas, USA. In: Rice Ratooning. IRRI, Manila, Philippines, pp. 257–264.
- Horie, T., Baker, J.T., Nakagawa, H., Matsui, T., 2000. Crop ecosystem responses to climatic change: rice. In: Reddy, K.R., Hodges, H.F. (Eds.), Climate Change, Plant Productivity and Global Implications. CABI Publishing, New York, NY, pp. 81–106.
- Imai, K., Cleman, D.F., Yanagisawa, T., 1985. Increase in atmospheric partial pressure of carbon dioxide and growth and yield of rice (*Oryza sativa* L.). Jpn. J. Crop Sci. 54, 413–418.

- IPCC, 2001. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., Van der Linden, P.J., Da, X., Maskell, K., Johnson, C.A., (Eds.), Climate Change 2001: The Scientific Basis. Cambridge University Press, New York.
- Jones, P.D., Wigley, T.M.L., Briffa K.R., 1994. Global and hemispheric anomalies: land and marine instrumental records.
  In: Boden, T.A., Kaiser, D.P., Sepanski, R.J., Stoss, F.W., (Eds.), Trends'93: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, pp. 603–608.
- Jones, P.D., Parker, D.E., Osbom, T.J., Briffa, K.R., 1999. Global and hemispheric anomalies—land and marine instrumental records. In: Trends: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN. (http://cdiac.esd.ornl.gov/ trends/temp/jonescru/jones.html).
- Keeling, C.D., Whorf, T.P., Wanlen, M., Van der Plicht, J., 1995. Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. Nature 375, 660–670.
- Kim, H.Y., Horie, T., Nakagawa, H., Wada, K., 1996. Effects of elevated CO<sub>2</sub> concentration and high temperature on growth and yield of rice. II. The effects on yield and its components of Akihikari rice. Jpn. J. Crop Sci. 65, 644–651 (In Japanese with English abstract).
- Kim, H.Y., Lieffering, M., Miura, S., Kobayashi, K., Okada, M., 2001. Growth and nitrogen uptake of CO<sub>2</sub> enriched rice under field conditions. New Phytol. 150, 223–229.
- Mann, M.E., Bradley, R.S., Hughes, M.K., 1999. Northern hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. Geophys. Res. Lett. 26, 759–762.
- Mathews, R.B., Kropff, M.J., Bachelet, D., Van Laar, H.H. (Eds.), 1995. Modeling the impact of climate change on rice production in Asia. CAB International in association with the International Rice Research Institute, 289 pp.
- Matsui, T., Namuco, O.S., Ziska, L.H., Hone, T., 1997. Effects of high temperature and CO<sub>2</sub> concentration on spikelet sterility in indica rice. Field Crops Res. 51, 213–219.
- Moya, T.B., Ziska, L.H., Namuco, O.S., Olszky, D., 1998. Growth dynamics and genotypic variation in tropical, field-grown paddy rice (*Oryza sativa*, L.) in response to increasing carbon dioxide and temperature. Global Change Biol. 4, 645–656.
- Murata, Y., Matsushima, S., 1975. Rice. In: Evans, L.T. (Ed.), Crop Physiology. Cambridge University Press, London, pp. 73–99.
- Pickering, N.B., Allen Jr., L.H., Albrecht, S.L., Jones, P.H., Jones, J.W., Baker, J.T., 1994. Environmental plant chambers: control and measurement using CR-10 dataloggers. In: Watson, D.G., Zazueta, F.S., Harrison, T.V. (Eds.), Computers in Agriculture, Proceedings of the 5th International Conference, Orlando, Florida, 5–9 February. ASAE, St. Joseph, Michigan, pp. 29–35.
- Reddy, K.R., Baker, J.T., Reddy, V.R., McKinion, J., Tarpley, L., Read, J.J., 2001. Soil–Plant–Atmosphere-Research (SPAR) facility: a tool for plant research and modeling. Biotronics 30, 27–50.
- Rowland-Bamford, A.J., Allen Jr., L.H., Baker, J.T., Boote, K.J., 1990. Carbon dioxide effects on carbohydrate status and partitioning in rice. J. Exp. Bot. 41, 1601–1608.

- Sasake, T., Hayase, H., 1970. Male sterility caused by cooling treatment at the young microspore stage in rice plants. 5. Estimations of pollen development stage and the most sensitive stage to coolness. Proc. Crop Sci. Soc. Jpn. 39, 473–486.
- Satake, T., Yoshida, S., 1978. High temperature-induced sterility in indica rice at flowering. Jpn. J. Crop Sci. 47, 6–17.
- Sheehy, J.E., Dionora, M.J.A., Mitchell, P.L., 2001. Spikelet numbers, sink size and potential yield in rice. Field Crops Res. 71, 77–85.
- Tingey, D.T., McVeety, B.D., Waschmann, R., Johnson, M.J., Phillips, D.L., Rygiewicz, P.T., Olzyk, D.M., 1996. A versatile sun-lit controlled-environment facility for studying plant and soil processes. J. Environ. Qual. 25, 614–625.
- Turner, F.T., Jund, M.F., 1993. Rice ration crop yield linked to main crop stem carbohydrates. Crop. Sci. 33, 150–153.
- Vu, J.C.V., Baker, J.T., Pennanen, A.H., Allen Jr., L.H., Bowes, G., Boote, K.J., 1998. Elevated CO<sub>2</sub> and water deficit effects on photosynthesis, ribulose bisphosphate carboxylase–oxygenase, and carbohydrate metabolism in rice. Physiol. Plant. 103, 327– 339.

- Widodo, W., Vu, J.C.V., Boote, K.J., Baker, J.T., Allen Jr., L.H., 2003. Elevated growth CO<sub>2</sub> delays drought stress and accelerates recovery of rice leaf photosynthesis. Env. Exp. Bot. 49, 259–272.
- Yoshida, S., 1972. Physiological aspects of grain yield. Ann. Rev. Plant Physiol. 12, 89–97.
- Yoshida, S., 1981. Fundamentals of rice crop science. International Rice Research Institute, Los Banos, Philippines.
- Ziska, L.H., Teramura, A.H., 1992. Intraspecific variation in response of rice (*Oryza sativa*) to increased CO<sub>2</sub>photosynthetic, biomass and reproductive characteristics. Physiol. Plant. 84, 269–276.
- Ziska, L.H., Manalo, P.A., Ordonez, R.A., 1996. Intraspecific variation in the response of rice (*Oryza sativa*. L.) to increased CO<sub>2</sub> and temperature: growth and yield response of 17 cultivars. J. Exp. Bot. 47, 1353–1359.
- Ziska, L.H., Namuco, O., Moya, T., Quilang, J., 1997. Growth and yield response of field-grown tropical rice to increasing carbon dioxide and air temperature. Agron. J. 89, 45–53.